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ADAPTATION IN BONE ARCHITECTURE¹

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WE recognize two types of bone: compact and cancellous. In flat bones we have the latter as the diploe between two layers of compact bone. In long bones there is a tubular structure of compact bone with a varying amount of cancellous bone inside.

For instance, in the human femur, the shaft portion is a tube with a wall of compact bone which is thick except near the ends; here the compact bone becomes thin and is continued over the swollen ends of the femur as a thin layer. In the shaft region of the femur, the cancellous portion is represented by relatively few and widely separated bone trabeculae. The space inside the tube of compact bone is occupied mostly by marrow. In the enlarged end portions of the femur, a complicated system of crowded trabeculae produces a spongy structure with small interspaces.

The enlargements at the ends of the femur furnish needed surface for the attachment of muscles, tendons and ligaments. They are also important in the joint mechanism. The spongy structure permits an enlargement without increased weight.

The central spaces, even though occupied by marrow, give the bone some of the architectural advantage of a tube over a solid rod, *i. e.*, greater rigidity or resistance to bending strain than is possessed by a solid structure of the same length and weight of material.

In many birds, and especially in some larger forms, this architectural advantage has been carried still further, and we have decidedly hollow bones with no heavy marrow. Even the bone trabeculae have disappeared more or less completely, and the hollow spaces are occupied by evaginations from the lungs, the air sacs. The extent of this pneumatization of the bones varies, but in a bird like the albatross it is extraordinary. The vertebrae with all of their intricate contour are hollow, and these air spaces extend into the smallest processes. There is no solid bone much thicker than writing paper except in the

¹ An address at the University of Illinois Summer Graduate School of Medicine, Aug. 30, 1917.

leg bones. The skull may be said to have thin layers of compact bone separated by an extensive diploe which has its bony elements often reduced to slender spicules with very large air spaces instead of marrow. The bones of the albatross are consequently exceedingly light in weight.

Bones containing air spaces are not confined to birds. In mammals, we have air sinuses in the skull which are connected with the respiratory tract and are lined with membranous extensions from the respiratory passages. Such sinuses are especially well developed in the skulls of the larger ungulates, and they are familiar structures in man. In a group of fossil reptilia, the Dinosaurs, pneumatization of the skeleton was apparently developed as far as in any of the birds, and possibly more.

In spite of their apparently frail structure, I have found albatross bones surprisingly strong and capable of withstanding relatively severe tensile and compressive strains. Their factors of safety are large. Thus the articular processes of the vertebræ resist bending strains of great severity. Though the amount of real bone tissue present is small, and the bulk of the vertebra is air space, a pull of 28 to 42 pounds applied in the most critical direction was necessary to produce fracture. This strain was, furthermore, not in any direction that tensile or bending strains would be likely to take in nature. Pressures of twenty to thirty kilograms applied to the vault of dry skulls from young albatrosses of a small species produced a crack in the sphenoidal region, but no rupture of the vault. These figures underestimate the strength of most parts of the albatross skull in spite of its great lightness and pneumaticity.

Tests of fresh normal human compact bone by Hülsen² and by Rauber³ indicate its very great strength and are illuminating here. Thus a tensile strength of $9\frac{1}{4}$ kilograms per square millimeter, or 13,000 to 17,000 pounds per square inch, was found. The compressive strength is still greater, the figures varying from $12\frac{1}{2}$ to about 19 kilograms per square millimeter or 18,000 to nearly 20,000 pounds per square inch. The following factors of safety for various parts of the human femur in running are given by J. C. Koch in an excellent paper on bone architecture.¹ For tensile strength, the variation is between 5.68 at the weakest point in the neck to 53.6 in the head. For compressive strength, the figures vary between 5.1 in the neck

² Jahresber. d. Anat. u. Entwick, 1898, Bd. I, p. 146.

³ Elasticität und Festigkeit der Knochen, Leipzig, 1876.

¹ *Am. Jr. Anatomy*, March, 1917.

to 119.5 near the proximal end of the femur. These figures are doubled for walking, but are very much less in the case of impact due to jumping or falling. However, there are of course compensatory movements of muscle contraction and flexing of joints which offset the effect of impact more or less.

The strains due to muscle contraction are ordinarily much less than those due to loads or to impact. Thus Koch states that the greatest possible contraction of the thigh muscles would "develop only about one seventh of the strength of the femur." He also says that the tensile strength of bone is about 230 times that of muscle. In various tests that I have made, using a steady pull, I have found that muscles and tendons will break before any significant strain is placed on even such slight structures as the cervical ribs of an albatross vertebra. I have not found any way of measuring the strains which muscles and tendons actually exert in normal activity, but they must be far within the factor of safety.

Nevertheless, there are some curious contradictory facts in clinical records. Thus Stimson in his book on "Fractures and Dislocations" mentions various fractures which were the result of muscular action. An athletic man broke the humerus of his throwing arm just below the insertion of the deltoid, in throwing a stone. The femur has been broken in attempts to kick, to avoid a fall, in drawing on a boot, or in turning over in bed. A primipara broke her sternum in labor, trying to assist the action, rising on her heels and elbows. Fractures of the patella from muscular action are not uncommon, and they also occur at the tuberosities of the long bones where powerful muscles are attached.

I recall a fracture of one of the long bones of the wing of a gull struggling to free itself from my grasp. My hold happened to slip to one wing for a moment. Ordinary tests of the wing-bone resistance to bending strain do not suggest such a possibility.

Apparently, sudden and violent contractions of groups of muscles may produce strains greatly in excess of our measurements. Surprising feats of strength are performed under the influence of strong emotion or mania. The large factors of safety indicate provision for unusual as well as normal strains, but it is also obvious, as Stimson says, that "Nature's precautions are as a rule calculated upon the basis of the probable, not of the exceptional." These fractures evidently involve abnormal strains.

My tests have been made with dead tissue. I have used both

fresh and fixed material, and I know of no data concerning the relative strength of living and dead tendons or muscles. These cases of fracture of bones from muscle contraction and the unusual feats of strength just mentioned suggest that muscle tissue may possibly have in life a greater strength than immediately after death. The tests I have made were simple and involved tying a string about the muscle or tendon, with the other end fastened to a spring balance which was subjected to a steady pull. The following tests were made with albatross tendons from formaline fixed specimens. Tendons of the longus colli muscle inserting on cervical ribs at about the middle of the neck broke under a pull of four to five kilograms. A biventer cervicis tendon ruptured under a strain of about two and one half kilograms. A small species of albatross, *D. nigripes*, was used. Fresh longus colli tendons attached to cervical ribs at about the middle of the neck of a gull, ruptured under a pull of one and one half to two and one half kilograms. Such results indicate large factors of safety for these structures. Most of the albatross cervical vertebræ, for instance, receive a pair of longus colli tendons. Neither the weight nor the habits of the albatross would seem to require, even in emergencies, such large factors of safety; yet they are probably not larger than is necessary for occasional but not very rare strains.

Much has been written about the remarkable adaptations in the human femur to its functions as well as those of other bones. We may mention especially the publications of Roux,⁴ Julius Wolf⁵ and J. C. Koch. The paper by Koch mentioned earlier in this paper puts the subject on a sounder and more mathematical basis than it was.

Longitudinal sections have demonstrated that the trabeculæ of the proximal end of the femur, for instance, are arranged in series which cross each other at right angles. Furthermore, these trabeculæ have been shown to have the direction of the lines of maximum tensile and compressive strength. They are arranged to meet the severe strains which the femur experiences, normally, and they involve a great economy in material. The efficiency of such a bone is well indicated in the following quotation from Koch: "The various parts of the femur taken together form a single mechanical structure wonderfully well adapted for the efficient, economical transmission of loads from the acetabulum to the tibia; a structure in which

⁴ Biol. Centralbl. 1881, Bd. I; also Zeitschr. f. orthopaed. Chirurgie, 1895-6, Bd. 4, p. 284.

⁵ Das Gesetz der transformation der Knochen, 1892, Berlin.

every element contributes its modicum of strength in the manner required by theoretical mechanics for maximum efficiency."

The publications of Wolff and of Roux have given us a large amount of data illustrating the possibilities of bone adaptation under exceptional conditions. In cases of fracture with imperfect coaptation and in disease, remarkable rearrangements of bone structure to meet new conditions occur. Thus Wolff has described cases of extra-capsular fracture of the femur through the neck and greater trochanter. In one case, some of the medial cortex of compact bone belonging to the upper fragment was driven into the cancellous bone of the lower fragment. In the union that followed, adaptive rearrangements of trabeculae to meet tensile and compressive strains occurred. Likewise in another case where compact bone from the lower fragment on its medial side was driven into the cancellous bone of the upper fragment, adaptive rearrangements of trabeculae followed. Local thickenings of the cortical compact bone also occur in such cases.

In fractures which involve widely separated fragments, bony bridges are formed. These involve large readjustments of both external form and internal architecture.

In a remarkable case described by Roux,⁶ a false joint developed as a consequence of imperfect union of a fractured bone. The fracture was of the tibia at the juncture of its upper and middle thirds. This was followed by an extensive hypertrophy of the fibula which became larger than the tibia and took over its functions. The tibia suffered an actual reduction in size. The fibula also increased in length so that it formed an articulation with the lateral condyle of the femur. The enlargement of the femur is said to have involved the formation of normal healthy bone.

Other fractures have been studied in such detail, and the results have been similar in demonstrating transformations to meet new conditions.

In ankylosis of joints, a remarkable unbroken continuity of the trabeculae of the two fused bones, may be established. This involves a reorganization of the cancellous bone. Changes in the thickness of the compact bone take place at points far removed from the anchylosing joint.

The well-known effects of unusual or excessive strains or loads upon developing bone involve deformities which have also been shown to undergo changes in architecture. From this

⁶ Biol. Centralbl., 1891, Bd. I, pp. 241-51. See also Julius Wolff, 1892, *Das Gesetz der Transformation der Knochen*, Fig. 49, Taf. VII.

knowledge has arisen the practice of orthopedic surgeons of removing a deformity producing load or strain and the use of corrective treatments involving artificially applied loads or strains.

This adaptiveness of bones to new conditions has not been generally realized by biologists, I believe. It was not known to me until very recently, and it has suggested to me some reflections concerning the origin of bone architecture. Let us review briefly the principal doctrines of evolution and discuss the bearing of bone adaptation on them.

Though natural selection has undoubtedly been an important factor in the evolution of the skeleton, it is likely that other factors have been more potent. Recent opinion holds natural selection insufficient to account for the enormous progress of evolution. Many believe that it does not originate characters, but simply favors more suitable variations while rejecting the unfit.

It is difficult to conceive of all the complex organization of the femur for its functions as a consequence of sudden changes or mutations, even though we grant the possibility of more than one mutation in the same direction.

In orthogenesis, we have an interesting viewpoint. It is easy to think of continuous variation in a definite direction as potent in evolution when we see fine series of intermediate stages. Unfortunately, there has been much vagueness about this hypothesis. Various opinions have been expressed as to what the motive principle may be. We have had various kinds of orthogenesis with intimate relationships to other evolution doctrines. The hypothesis of Nägeli is generally classed as orthogenetic. Greater perfection, more complex organization, greater division of labor, perfection of adaptation were believed to be principles of the organism. A perfecting principle carried by the germ cell was the central idea. The germ plasm has an organization which tends to produce variation in the direction of the most advantageous structure which is compatible with its degree of structure, of complexity and division of function.

The late Professor Whitman was much impressed with Nägeli's conception and he worked out a hypothesis not very different from that of Nägeli. According to Professor Whitman, the germ plasm may contain some condition of its organization which is responsible for continuous cumulative variation. In breeding experiments with pigeons, for instance, he obtained evidence that variation has been in the direction

of a barred pattern from an originally checkered pattern. Professor Whitman was sceptical concerning the possibility of environmental changes being effective. He had been for many years an embryologist and was naturally influenced by the ably supported doctrine of Weismann: the continuity of the germ plasm.

Unfortunately for orthogenesis, we have no data, and in fact hardly even a guess, as to what the germ plasm attributes may be which would be responsible for orthogenesis.

Since the announcement of Weismann's continuity of the germ plasm, there has been a curious division among biologists concerning the so-called Lamarckian doctrine of evolution as the consequence of inheritance of acquired characters. We know that much of this disagreement has been due to a failure to agree on what constitutes an acquired character. There has been some loose thinking and much quibbling. Furthermore, viewpoints have been too limited and data too meager. Accepting the embryological viewpoint that an acquired character is somatic, we have biologists with a large embryological horizon referring all evolutionary progress to the germ cells. On the other hand, paleontologists with the marvelous adaptations of the skeleton constantly before them have remained defenders of the importance of environmental factors, of use and disuse.

To a certain extent, it must be admitted, the paleontologists have been ignorant of, or oblivious to, the exceedingly strong evidence which supports the conception of continuity of the germ plasm. On the other hand, I believe that this doctrine has been too sweepingly asserted by the embryologists, and I think that the truth lies between these viewpoints.

Of course we can not deny that in sexually reproducing organisms the fertilized egg must contain all the factors for characters not actually acquired by the individual in ontogeny. The question is can a somatic change, for instance an alteration in the femur, be transmitted to the offspring. To provide for the germ cell equipment that must be involved we recall various hypotheses of pangenesis involving ultra microscopic particles, gemmules, etc. So far, at least, these attempts have not emerged from the field of pure speculation.

Sounder conclusions are to be expected from work in experimental evolution, but the dangers of false interpretation are great. There are confusing intricacies and numerous uncertain factors to trip up the investigator. Long periods of time are apparently necessary for significant results.

"The brilliant progress in heredity of recent years, beginning in 1903 with the rediscovery of Mendel's law, should not blind us to the four broad deductions from paleontology, that transformation is a matter of thousands of years, that to the living observer all living things may be delusively stationary, that invisible tides of genetic change may be setting in one direction or another observable only over very long periods of time, that discontinuous mutations or saltations may be mere ripples on the surface of these tides."²

Until very recently, experiments testing the effects of environmental changes have mostly given doubtful evidence of transmission of new characters to the offspring. Usually, each generation has apparently had to start where the parents began. Nevertheless, the results have not all been negative. Thus Tower has obtained inherited alterations in pigmentation of potato beetles as the consequence of changed environmental conditions during the period of germ-cell development. Experiments on the effects of alcohol on the offspring when given to the parents, MacDougal's work with plants, and other experimental work recently done, all indicate susceptibility of the germ cell to external stimuli. One clear undisputed case alone of such susceptibility to external stimuli which is potent in inheritance, *i. e.*, results in new characters for the offspring, should be sufficient to overthrow the dogmatic assumption that the germ plasma can not be affected by changes in the environment so far as heredity is concerned.

The germ cells are not hermetically sealed in the gonads. There is no evidence that they are not reached freely by the blood stream with its contained internal secretions and various unknown elements. We have had much new evidence recently of the intricate and extensive relationships of tissues to each other, physiologically. The form in which influences reach the germ cell is unknown to us, but so are the agents of many other biological phenomena which we know exist. It is not improbable that the factors which are responsible for changes, in the femur, for instance, are associated with the cell organization.

Adaptation phenomena are more numerous than we often realize. Temperature control, regeneration and regulation processes are examples of adaptation. The activities of phagocytes and some of the wonderful phenomena of immunity are also illustrations. If a bone is broken, osteoblasts inactive for years and ordinarily destined to remain idle resume inactivity, and other bone-forming processes begin. We do not know what are the agencies which start these activities, but the results are obvious enough.

² H. F. Osborn, *Am. Nat.*, April, 1912, pp. 185-6.

Possession of an adaptation does not insure supremacy or survival. Another competitor may have a better adaptation. Not all advantages in the struggle for existence are possessed by a single organism. Many individuals of various species and groups are in complex competition with each other. Adaptations are furthermore subject to the limitations of heredity and environment. An automobile can not fly nor can a locomotive swim, yet both are highly adapted to their functions.

The occurrence of apparently useless or even disadvantageous characters has been used as an argument against characters being adaptive. Characters apparently highly adaptive have been explained as accidents of development or of evolution. All such arguments are beside the mark. They involve a failure to consider other forces and principles in their relationships to adaptiveness as a characteristic of protoplasm. Adaptive tendencies may be handicapped by other tendencies or forces. Heredity may preserve a character past the period of its usefulness.

We have had much new evidence in recent years of the amount of adaptiveness possessed by lower organisms. Even the ameba has been shown to be more resourceful than was at one time suspected. The more elaborate the organization, the more varied and effective are the adaptations.

The problem of explaining the origin of adaptation is made difficult because changes beyond what may be acquired in a single generation are inhibited by the *conservative forces of heredity*. In the germ cell we find permanency. There are located all those forces involved in heredity which preserve the type. Germ plasm tends to beget the same plasm. Ultra Mendelianists have even gone so far as to deny the possibility of any evolution except by recombinations or losses of germ plasm units. The mutationists account for mutations as the result of small spontaneous germinal changes. These writers, and especially the Mendelianists, are over impressed with the precision and scope of heredity. They fail to recognize the *interplay between heredity and adaptation*..

It is not easy for the organism to break away from its inheritance, especially in certain characters. Furthermore, it is conceivable that adaptations reach limits or that heredity may become too strong for a change to occur, even with great environmental changes. In fact, it is difficult to explain the failure of lower organisms to have evolved further than they have on any other basis. I believe that there is much significance in the old idea of varying degrees of plasticity with regard to sus-

ceptibility to environmental changes. Some adaptations are doubtless easier than others, and changes in certain directions may be easier than in others. The strength of heredity may increase when the environment remains relatively constant for long periods of time.

It is quite unnecessary and entirely unwarranted to ascribe a teleological basis for adaptation. It does not make the situation clearer to talk of entelechies or to assume a so-called vitalistic principle. We have no evidence that an adaptation is the consequence of any entities or properties different essentially, except possibly in complexity, from the characteristics of simple chemical compounds. Bone architecture may be said to be the consequence of physico-chemical processes which include among other *competing* activities, adjustments to the needs of the organism.

SUMMARY

Skeletal structures are capable of much greater changes than biologists ordinarily realize. Bones are highly adapted to their functions. Their architecture may be greatly altered as the consequence of accidents, new strains or disease.

The viewpoint is maintained in this paper, that the organism and its constituent cells have as a condition or principle of their organization adaptiveness to new conditions. This involves susceptibility to stimulation effective in heredity. There is evidence that this capacity is possessed by the germ cells as well as by the somatic cells. The doctrine of absolute isolation of the germ cells from stimulation by somatic cells which may be effective in heredity, is untenable. Much of this apparent isolation or lack of susceptibility may be due to the power of the conservative forces of heredity.

The balance in power between heredity and environmental influence may be considered to vary for different characters and organisms, very likely also for periods in activity. In the course of time, a character may become fixed, or mechanical limits may be reached for adaptation.

The architecture of the skeleton is regarded as the consequence, to some extent at least, of inherited adaptations.

The phenomena of bone architecture development and adaptation do not appear to support the ultra-Mendelian conception that new characters can arise only by recombinations of unchangeable germ-plasm units or by the loss or addition of such units.